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A SYSTEMATIC STUDY OF THE SALICACEÆ.

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IN attempting a discussion of the Salicaceæ from the stand-
point of their ancestry, as presented in the woody structure of
the mature stem, a first step involves comparison with previously
existing forms and with closely related types now extant, in
order to determine the general phylogenetic sequence and the
position which the group at present occupies. We are there-
fore led, at the very outset, to ask : (1) what is the nature of
the evidence to be derived from paleontology, and what is the
bearing of such evidence ; and (2) what is the nature and bear-
ing of the evidence to be derived from the structure of existing
species ? The Salicaceæ as we now know them, are altogether
confined to two genera — Populus and Salix — of very wide
distribution in north temperate latitudes whence they extend
beyond the extreme northern limit of tree growth within the
polar circle, being there reduced to prostrate shrubs. It is
quite possible that the family may have been more extensive in
early or middle Mesozoic time, but the evidence now available
as derived from their fossil remains, leads us to the supposition
that it has not been, at any previous time in its history, of a
more comprehensive character. In common with many other

families of Dicotyledons, it made its appearance very abruptly
in the Cretaceous age, whence it has continued through suc-
ceeding formations, appearing with prominence in the Pleis-
tocene where its remains form a distinctly connecting link with
existing species, with many of which they are more or less
identical.

An analysis of the Salicaceæ based upon the enumeration
of the Index Kewensis, shows that there are at the present time
no less than two hundred and seventy recognized species, an
altogether unusual proportion for a family embracing such a
limited number of genera.   Of these, twenty-two belong to the
genus Populus, while two hundred and forty-eight belong to the
genus Salix.

The poplars are preëminently a type peculiar to the northern
hemisphere, and in their chief aspects they have a strong tend-
ency to a boreal habit, the one exception to be met with in
the subtropical *P. mexicana* offering no material contradiction
of this law.   *P. ciliata* of the Himalayas, though reaching a
latitude far below that of most representatives of the genus,
nevertheless conforms to the temperate habit of the group by
virtue of the somewhat high elevations at which it grows.   Six
species range from Japan through China, Mongolia, and Siberia
to Central Asia, while the western extension of the genus is
carried through northern and central Europe as far south as
Spain and Italy.   In the western hemisphere, no less than ten
species are to be met with, ranging from Mexico as the extreme
southern extension, thence northward as far as the arctic circle
where *P. balsamifera* appears to establish the limit of develop-
ment.   The very remarkable isolation and localization of the
various species is one of the most prominent features disclosed
by an examination of these plants.   *P. mexicana* is confined to
Mexico and similarly *P. ciliata* is peculiar to the Himalayas.
P. adenopoda is restricted to China as *P. sieboldii* is to Japan ;
while *P. przewalskii* of Mongolia and *P. pruinosa* of Siberia, as
also *P. euphratica* of Central Asia, give emphasis to this strong
segregation, since they are as wholly distinct from the European
and American species as are those of the last two regions from
one another.   In only one instance does there seem to be any

connecting form. This is presented in the ubiquitous balsam poplar of Asia and North America which not only serves to connect the types of both hemispheres, but it gives to the genus a greater range of latitude than any other species. Evidence of this nature would naturally lead to the supposition that *P. balsamifera* may represent a more generalized type ancestral to many of the associated species. But on the other hand, the very extensive distribution of distinct species occupying essentially isolated and often very widely separated regions, suggests a more general dispersal during Cretaceous and Tertiary time, and their eventual restriction to more limited areas through the operation of important physical agencies, with the survival of the more resistent but not necessarily the oldest species. In particular it is conceivable that such restriction may have been brought about in one of two ways : (1) the elimination of the ancestral type or types, of which *P. balsamifera* may possibly be regarded as the sole survivor, would tend to leave the descendants isolated as now found ; (2) the ancestral forms having disappeared at a comparatively early period in the history of the genus, more recent physical changes in the earth's crust and in climatic conditions would give rise to more or less profound alterations in distribution in such a way as to effect a more pronounced segregation and localization. That such causes have been operative in glacial times is well known, and they have left a very definite impress upon the distribution of the existing flora of this continent, as particularly indicated by the various forms of alpine vegetation (Gray, '89, vol. 1, p. 122 ; vol. 2, pp. 24, 142, 260) and by such special arborescent forms as *Larix americana*, Sequoia, *Pseudotsuga douglasii*, etc. (Penhallow, : 04).

From this analysis it appears that there are twelve species of poplar peculiar to the Old World and nine species peculiar to the New World, with one species common to both. From this circumstance it would be natural to conclude that this is essentially an Old World genus, but the slight numerical difference noted would make such a generalization unsafe without confirmatory evidence derived from the paleontological record to which appeal must also be made for an answer to several other questions that have already arisen.

Like the poplars, the willows are a type essentially peculiar to the temperate regions of the northern hemisphere, though they represent adaptation to a greater diversity of climatic conditions and thereby greatly extend the northern and southern range of the family as a whole.   With the exception of about 2 percent —an altogether insignificant proportion—they are of a continental character.   Nevertheless, in the *S. junghuhniana* of Java, *S. sumatrana* of Sumatra, *S. canariensis* of the Canary Islands, *S. madagascariensis* of Madagascar, and *S. occidentalis* of the West Indies, types which are strongly segregated and localized, their very restricted range is in close proximity to the corresponding vegetation of the continental areas in which they must have had their origin and from which they must have been isolated at a comparatively late period as shown by Wallace ('80). It is these insular forms which are chiefly concerned in the extreme southern extension of the genus, since the six Mexican and eight north African species range considerably farther north. The extreme isolation of *S. humboldtiana* in South America affords at once an illustration of the extent to which dispersal must have been carried in former geological times, and of the potency of the influences which have tended to a greater restriction of geographical area.

Of the one hundred species common to Asia, twenty-four are found within the Himalayan region, while seventy-three are more peculiar to the temperate and boreal regions of Japan, China, Siberia, and Central Asia.   In Europe no less than eighty-four species give a range to the genus which extends from the Mediterranean on the south to the polar regions where the very diminutive *S. polaris* with an extreme height of about 3.3 cm., defines the northern limit of growth.   In North America, apart from Mexico, seventy-two species similarly extend the genus over a wide range of latitude, their northern limits being defined by the boreal *S. ovalifolia* which also ranges southward on the summits of lofty mountains, as far as Mount Washington in New Hampshire.   Ubiquitous species are much more common than among the poplars, and there are no less than 23 which are more or less common to the several continental regions as exhibited by the following synopsis.

Community of Species of Salix.

Europe and Asia	14
Europe and North America	7
Europe and Africa and Asia	1
Asia and Africa	1
	—
	23

In determining these relations, the very pronounced isolation of the Japanese and Himalayan species stands out with great prominence and lends emphasis to the idea of segregation in a previously continuous flora.   From the facts thus presented, it is obvious that the willows are preëminently an Old World genus, and that, although their dispersion has a tendency to greater diffuseness than in the case of the poplars, like them they essentially belong to temperate regions, and their tendency is on the whole boreal, rather than austral; so that with respect to the Salicaceæ as a whole, it may be said to be a distinctly temperate and boreal family of wide dispersion within the northern hemisphere, with its center of distribution in Asia where it presumably had its origin.   A summary of these geographical relations will serve to make the foregoing analysis more clear.

In the light of these facts it becomes pertinent to ask whether the family as now known represents a type of vegetation which is yet in process of evolution, if it is a side line which has recently attained to the full limit of development and which is therefore terminal, or if it attained the culmination of its development in some previous geological age and is now in a state of decline comparable with that exhibited by the Lycopodiaceæ and the Equisetaceæ.   The comparatively recent origin of these plants, if we are to judge them by the standards which have been set by other groups, the general phylogeny of which is fairly well known, would naturally lead us to support the first hypothesis or at least the second, and to reject the third as improbable.   But such generalizations are unsafe unless supported by other well established data, and it therefore becomes necessary to inquire somewhat particularly into the nature of the evidence afforded by the geological history of these plants.

Geographical Distribution of the Salicaceæ.

	Old World.									New World.			
	Malaya.	Java.	Sumatra.	India. Himalayan Region.	Other parts of Asia.	Madagascar.	Canary Islands.	Africa.	Europe.	South America.	West Indies.	Mexico.	North America.
Salix	1	1	1	24	73	1	1	8	84	1	1	6	72
	100					10			84	80			
248	194									80			
Percent	0.4	0.4	0.4	9.68	29.43	0.4	0.4	3 22	33.87	0.4	0 4	2.41	29.03
	40.32%					4.03%			33.87%	32.26%			

	Old World	New World
	78.22%	32.26%
Duplications	8.19%	2.19%
Total	70.03%	29.97%

	Old World.									New World.			
Populus				1	6				6			1	9
22	13									10			
Percent				4.54	27.27				27.27			4.54	40.91

	Old World	New World
	59.09%	45.45%
Duplications	2.68%	1.86%
Total	56.41%	43.59%

	Old World	New World
Salicaceæ	78.88%	33.33%
270 Duplications	9.63%	2.58%
Total	69.25%	30.75%

Our knowledge of the fossil Salicaceæ had its origin in the work of Heer upon the fossil plants from the Cretaceous formation of Greenland, through his description of *Populus primæva*. The occurrence of this species in the Kome beds not only afforded the first real evidence of the occurrence of these plants in previous geological time, but it at once served to suggest the essentially primitive character of the Salicaceæ as a whole among Dicotyledons—an idea subsequently strengthened by the discovery of both Salix and Populus in the Potomac formation, as well as in the Kootanie beds of Montana. This idea, then, has persisted to the present day and finds repeated expression in the various treatises on fossil plants, although the acceptance of such a view is not based in any case, upon trustworthy facts derived from a critical comparison of distribution, a knowledge of the phylogeny of the group, or an acquaintance with the anatomy of either recent or extinct species. Paleontologically it is of interest to determine the position of the Salicaceæ relatively to the other families associated with it in the Cretaceous and Tertiary deposits, and for this purpose the flora carefully compiled by Dr. Knowlton ('98) offers the most reliable basis now available. Among forty-five families of angiosperms now known to constitute the flora of the Cretaceous and Tertiary ages in North America, it will be found that, geologically speaking, the Salicaceæ is by no means the primitive group which seems to be implied by the position usually assigned to it, but that it really occupies a position which is the twenty-fourth in a series based upon the percentage ratio of occurrence in the two great geological periods. Such a series has as its lowest member, the Proteaceæ which is preëminently a Cretaceous family, bearing to the Tertiary the ratio of 19 : 0. The same is also true of the Menispermaceæ with a ratio of 17 : 0, closely followed by the Araliaceæ (6 : 0) and the Euphorbiaceæ (2 : 0). At the other extremity of the series we find such families as the Hydrocharidaceæ (0 : 2), Lemnaceæ and Simarubaceæ (0 : 3), Typhaceæ (0 : 4), Onagraceæ (0 : 5), Naiadaceæ (0 : 7), Zingiberaceæ (0 : 17), and the Cyperaceæ (0 : 20), all of which are manifestly typical Tertiary plants. About midway of the series the Salicaceæ are associated with the Urticaceæ with a ratio of 1 : 1.47 and with the somewhat similarly distributed Platanaceæ,

Myricaceæ, Cornaceæ, and Sapindaceæ. There is thus a very strong suggestion (1) that the Salicaceæ is in no sense a primitive family from the standpoint of geological succession, and (2) it is, as a whole, much more characteristic of the Tertiary than of the Cretaceous, more especially as a closer analysis of the one hundred and forty-one known species shows that this rule applies to each of the constituent genera as well as to the entire family, though more conspicuously to the genus Populus than to Salix. Thus we find that the forty-seven Cretaceous species embrace 34 of Populus and 23 of Salix, while the eighty-four Tertiary species embrace 59 of Populus and 25 of Salix, making the ratio of Cretaceous to Tertiary 1 : 1.75 for the former and 1 : 1.09 for the latter — ratios which tend to indicate that these two genera and so the family as a whole, were in process of development even in Tertiary time, a conclusion which is in apparent accord with the recent origin of the family.

Comparison of Cretaceous and Tertiary Floras.

	Seq. No.	Ratio.	Cretaceous		Tertiary	
			No.	Percent.	No.	Percent.
Proteaceæ	1	19 : 0.00	19	1.09	0.00	0.00
Menispermaceæ	2	17 : 0.00	17	0.98	0.00	0.00
Araliaceæ	3	6 : 0.00	6	0.34	0.00	0.00
Euphorbiaceæ	4	2 : 0.00	2	0.11	0.00	0.00
Passifloraceæ	5	1 : 0.00	1	0.06	0.00	0.00
Asclepiadaceæ	5	1 : 0.00	1	0.06	0.00	0.00
Myoporineæ	5	1 : 0.00	1	0.06	0.00	0.00
Convolvulaceæ	5	1 : 0.00	1	0.06	0.00	0.00
Bromeliaceæ	5	1 : 0.00	1	0.06	0.00	0.00
Casuarineæ	5	1 : 0.00	1	0.06	0.00	0.00
Sterculiaceæ	6	1 : 0.13	15	0.86	2	0.11
Myrsineæ	7	1 : 0.17	6	0.34	1	0.06
Myrtaceæ	8	1 : 0.18	11	0.63	2	0.11
Hamamelaceæ	9	1 : 0.25	4	0.22	1	0.06
Magnoliaceæ	10	1 : 0.31	45	2.60	20	1.15
Thymeleaceæ	11	1 : 0.33	3	0.17	1	0.06
Anonaceæ	11	1 : 0.33	3	0.17	1	0.06
Araliaceæ	12	1 : 0.36	47	2.71	17	0.98
Sapotaceæ	13	1 : 0.50	4	0.22	2	0.11
Lauraceæ	14	1 : 0.56	69	3.98	39	2.25
Vitaceæ	15	1 : 0.61	26	1.50	16	0.92

	Seq. No.	Ratio.	Cretaceous		Tertiary	
			No.	Percent.	No.	Percent.
Celastraceæ	16	1 : 0.70	30	1.73	21	1.21
Leguminosæ	17	1 : 0.72	32	1.84	23	1.32
Araceæ	18	1 : 0.75	4	0.22	3	0.17
Ebenaceæ	19	1 : 0.76	13	0.75	10	0.57
Ericaceæ	20	1 : 0.94	18	1.03	17	0.98
Bignoniaceæ	21	1 : 1.00	1	0.06	1	0.06
Apocynaceæ	21	1 : 1.00	1	0.06	1	0.06
Alismaceæ	21	1 : 1.00	2	0.11	2	0.11
Platanaceæ	22	1 : 1.26	15	0.86	19	1.09
Myricaceæ	23	1 : 1.29	24	1.38	31	1.79
Urticaceæ	24	1 : 1.47	65	3.70	96	5.54
Salicaceæ	24	1 : 1.47	57	3.29	84	4.79
Cornaceæ	25	1 : 1.50	12	0.69	18	1.03
Sapindaceæ	26	1 : 1.62	24	1.38	39	2.31
Cupuliferæ	27	1 : 1.71	94	5.43	161	9.30
Caprifoliaceæ	28	1 : 1.82	17	0.98	31	1.79
Rhamnaceæ	29	1 : 1.96	26	1.50	51	2.94
Aquifoliaceæ	30	1 : 2.00	9	0.51	18	1.03
Aristolochiaceæ	30	1 : 2.00	2	0.11	4	0.22
Tiliaceæ	30	1 : 2.00	1	0.06	2	0.11
Rosaceæ	31	1 : 2.89	9	0.51	26	1.50
Juglandaceæ	32	1 : 3.00	13	0.75	39	2.25
Liliaceæ	32	1 : 3.00	2	0.11	6	0.34
Altingiaceæ	33	1 : 4.00	1	0.06	4	0.22
Nymphæaceæ	34	1 : 6.00	2	0.11	12	0.69
Gramineæ	35	1 : 6.50	2	0.11	13	0.75
Anacardiaceæ	36	1 : 7.50	4	0.22	30	1.73
Palmaceæ	37	1 : 18.0	1	0.06	18	1.03
Musaceæ	38	0 : 1.00	0	0.00	1	0.06
Eriocaulonaceæ	38	0 : 1.00	0	0.00	1	0.06
Elæagnaceæ	38	0 : 1.00	0	0.00	1	0.06
Droseraceæ	38	0 : 1.00	0	0.00	1	0.06
Rutaceæ	38	0 : 1.00	0	0.00	1	0.06
Polygonaceæ	38	0 : 1.00	0	0.00	1	0.06
Rubiaceæ	38	0 : 1.00	0	0.00	1	0.06
Berberidaceæ	38	0 : 1.00	0	0.00	1	0.06
Piperaceæ	38	0 : 1.00	0	0.00	1	0.06
Hydrocharidaceæ	39	0 : 2.00	0	0.00	2	0.11
Lemnaceæ	40	0 : 3.00	0	0.00	3	0.18
Simarubaceæ	40	0 : 3.00	0	0.00	3	0.18
Typhaceæ	41	0 : 4.00	0	0.00	4	0.22
Onagraceæ	42	0 : 5.00	0	0.00	5	0.28
Naiadaceæ	43	0 : 7.00	0	0.00	7	0.45
Zingiberaceæ	44	0 : 17.0	0	0.00	17	0.98
Cyperaceæ	45	0 : 21.0	0	0.00	21	1.21

The succession exhibited in this table brings into prominence the idea that such families as the Leguminosæ, Vitaceæ, Ericaceæ, Magnoliaceæ, Convolvulaceæ, etc., are inferior to the Salicaceæ which is, in turn greatly inferior to the Cyperaceæ from an evolutionary point of view when considered solely in the light of their geological succession ; but the sequence which is thus established is found to be utterly at variance with that usually adopted on the basis of morphological evidence which for obvious reasons must be regarded as the more trustworthy guide. Such discrepancies between the morphological and the geological succession, in our opinion, should not be so great as seem to be suggested by the available data, and no doubt they will diminish as our knowledge of the fossil representatives becomes more nearly complete, but that such discrepancies may be anticipated, and that they are to some extent to be regarded as a normal result of rapid evolution along many diverse lines of development, is a reasonable supposition. The Mesozoic age was a period of very great diversification among plants in consequence of the profound physical changes which had taken place in the atmosphere as well as in the configuration of the surface of the earth, and the fact that as a product of previous development, plants were in a condition to be widely and profoundly influenced by comparatively slight modifications of external conditions. The very great number of families and genera and even species of angiosperms which abruptly appeared in the Cretaceous, presenting as they did types of vegetation wholly unlike those of previous geological periods, indicates that the parental forms must have had their origin in the early Mesozoic and possibly as far back as the Permian, since our accept-· ance of the general principles involved in De Vries' mutation theory does not permit us to consider as possible, such phenomenal transitions as would be involved in the application of that theory to the case under consideration ; while on the other hand all paleontological evidence, as well as the evidence derived from existing types, confirms us in the belief that such highly organized forms could have arisen in the main, only through a long series of transitional forms occupying great periods of time. For the same reasons also, we are led to believe that the great

diversification of the Cretaceous flora must have been initiated
at correspondingly early periods, though the general succession
of types of which we have knowledge, would indicate that it did
not gain full expression until about the time of the Middle
Cretaceous.   This diversification was no doubt the natural
response of vegetation to the profoundly changed physical con-
ditions, chiefly climatic, which followed the close of the Carbon-
iferous age and resulted in a diminution of the carbon dioxide
of the atmosphere to about one-twentieth of its original volume
with a consequent reduction of atmospheric density ; a general
purification of the atmosphere whereby it became more readily
penetrated by the sun's rays ; a lower and less equable temper-
ature with more localized climates, and conditions which, as a
whole, were more favorable to a more varied mesophytic type of
vegetation.   Under such circumstances, involving as they did
a more abundant supply of oxygen, the general activities of
growth became greater ; the transformation of carbon dioxide
into assimilable products became proportionately larger ; in
response to the more favorable conditions of light and air, the
foliage became broader and acquired an increased functional
capacity ; and with the augmentation of capacity for the storage
of energy thus made possible, there were increased possibilities
of, as well as strong tendencies toward diverse development in
which special mutations no doubt played an important part, in
response to even comparatively slight variations in environmental
conditions.   From this point of view it is not difficult to under-
stand that among the numerous offshoots from the main line of
descent there would be very varying degrees of activity, and it
is readily conceivable that plants of a low phylogenetic position
might be held in numerical abeyance for a long time, while
others, originating at a higher level but more favorably situated
and more capable of responding to their environment, might at
once outdistance them in number of species or of varietal forms.
Under such circumstances the geological succession might lead
to erroneous conclusions as to the true phylogenetic sequence.
Such a view is suggested and supported by a comparison of
many well known examples among existing species.   In this
way it would be possible for a relatively superior type of organ-

ization, and one occupying a higher position in the morphologi-
cal scale, to occupy an inferior position in the geological scale,
and thus to appear antecedent to morphologically inferior types.

From the foregoing considerations it is clear that geological
data cannot be wholly relied upon to furnish a correct solution
of questions bearing upon the evolution of plant forms, and this
is especially true with respect to the broad-leaved angiosperms
for reasons which will be described more fully on a subsequent
page. Interesting as these various speculations may be, as
applied to the Salicaceæ they nevertheless lack an essential
foundation which can be obtained only by a more searching
scrutiny of the family as a whole, and of its component genera,
with respect to their more detailed distribution in Cretaceous
and Tertiary time, as well as at present.

Nowhere has it been possible to obtain so complete a record
of the Cretaceous flora as from the exposures to be met with in
Greenland and the United States, and the systematic way in
which the various horizons have been worked out, affords a very
satisfactory basis for a knowledge of the geological succession
of species and genera. In his studies of the Cretaceous flora of
Greenland, Heer found that out of a total of 88 species from
the Kome beds, only 5.68 % were Monocotyledons, while the
Dicotyledons were represented solely by *Populus primæva* to
the extent of 1.14 %. In the Cenomanian flora of the Atane
beds, there was a remarkable increase of Dicotyledons amount-
ing to 50.09 % in a total of 177 species; while from the Patoot
beds of the Senonian, 59.48 % were Dicotyledons out of a total
of 116 species, thus showing a marked development of this type
of plants toward the close of the Cretaceous. This ratio be-
tween the three divisions of the flora also appears to extend
very largely to the Salicaceæ in particular, with respect to
which we find 27.40 %, 42.40 %, and 30.10 % respectively for the
three horizons. An analysis of the family, however, shows that
this relation does not altogether hold in detail for the individual
genera. Thus in Salix the percentages are 41.40, 41.40, and
17.20 which approximates to the results for the family as a
whole with respect to the very evident falling off in the Upper
Cretaceous. Nevertheless this is much more marked in the

genus than in the family, and suggests that the former is in process of decline, a conclusion which seems to be directly opposed by the evidence afforded by the ratio of extinct and living forms. Populus gives 18.10 %, 43.10 %, and 38.60 % for the three horizons with a maximum development in the Middle Cretaceous.

Distribution of Salicaceæ in Cretaceous of United States.

SALIX.

	Lower.	Middle.	Upper.
Salix stantoni			×
mattawanensis		×	
meekii		×	
protæfolia	×	×	
" *flexuosa*	×	×	
" *lanceolata*		×	
" *linearifolia*		×	
" *longifolia*		×	
cuneata		×	
deleta		×	
hayei		×	
inequalis	×		
membranacea	×		
nervillosa		×	
newberryana	×		
pacifica			×
purpuroides	×		
sp.	×		
sp.			×
sp.	×		
sp.			×
sp.		×	
sp.			×
Saliciphyllum ellipticum	×		
longifolium	×		
parvifolium	×		
Species 26	11	12	5
Percentage distribution	42.3%	46.1%	19.2%

Distribution of Salicaceæ in Cretaceous of United States.

POPULUS.

	Lower.	Middle.	Upper.
Populus berggreni	×	×	
hyperborea		×	
stygia		×	
mutabilis	×		
lævigata			×
arctica			×
problematica			×
obovata			×
melanarioides			×
wardii			×
mutabilis ovalis ?			×
apiculata	×	×	
aristolochioides		×	
auriculata	×		
cordifolia		×	
elliptica		×	
harkeriana		×	
latidentata			×
kansaseana		×	
longior			×
leuce		×	
microphylla		×	
potomacensis	×		
protozadachi			×
rectinervata			×
rhomboidea			×
trinervis			×
sp.			×
sp.			×
sp.			×
Populites tenuifoiius		×	
cyclophylla		×	
elegans		×	
lancastriensis		×	
litigiosus		×	
microphyllus		×	
probalsamifera			×
sternbergii		×	
winchelli		×	
Populophyllum crassinerve	×		
hederæforme	×		
reniforme	×		
Species 42	8	19	17
Percentage distribution	18.1%	43.1%	38.6%

Again, comparisons with existing species are instructive. If all the various forms now recognized are to be regarded as valid species, then it would appear that the genus Populus must have attained to its full development in the later Cretaceous or possibly early Tertiary time, since when it has been in a process of slow decline, or at least it has made no substantial progress. A very noteworthy feature of such comparisons appears in the somewhat abrupt increase among the Salicaceæ in common with other Dicotyledons, in the Middle Cretaceous, especially in the Dakota group. A ready explanation of this phenomenon on purely botanical grounds might be found in the facility with which hybridization gives rise to very stable forms, and it is in all probability true that such hybridization is accountable in large measure for the multiplication of forms or species in past times as it is known to be at the present day ; but to the geologist this would probably not afford an adequate reason, since he recognizes the important extent to which " accidents " as determined by exposure of strata, methods of preservation, etc., constitute very definite and often controlling factors in the number and kinds of plants which may be yielded by a given formation, in which sense Dr. Knowlton has observed " that though some types of the Cenomanian, as shown by the leaves of the Dakota group, generally remain distinct and plainly defined in the vegetation of some of the subsequent formations, the chain of evidence is not always continuous. A number of these, for example, still remain unrecognized in the Upper Cretaceous, though present in more recent strata of the Laramie or of the Tertiary. We know very little as yet of the flora of the Senonian or of intermediate stages between the Dakota and the Laramie groups. But judging from recent discoveries in Wyoming, Montana, Canada, and Vancouver Island, we have been able to recognize in the scanty materials obtained, the presence and therefore the persistence of some of the primitive or more ancient types, and it is most probable that further research will complete the evidence of the persistence and representation of the types of the Dakota group up to the Laramie, as clearly as it is observable in this flora and through the different stages of the Tertiary to the present time (Lesquereux, '92).

We are now led to ask : "What is the nature of the evidence, with respect to the particular form and value of the plant remains, upon which our knowledge of the geological succession is based ? " Of the internal structure of the fossil Salicaceæ we as yet know nothing, for with the exception of a few specimens from the Pleistocene, the wood of these plants has not yet been brought under examination, and we are therefore denied one of the most definite means of distinguishing with certainty not only the various species and genera, but also the relations which the members of this group bear to one another and to other groups. That fragments of the stems of willows and poplars must sooner or later be found and brought under examination, is altogether probable, and as an essential provision for the proper recognition of the various species at such times, it is important that accurate diagnoses of existing species should be made.

The only evidence at present available for the recognition of members of the Salicaceæ, is in the remains of their leaves which are too often found in a very fragmentary condition and otherwise unsatisfactorily preserved. Recalling the extent to which hybrid and variable forms occur in this family, and the often extreme differences which may arise in the same species as shown by Ward ('88), Holm ('90, '95), Berry (: 01–: 03, : 02a, : 02b), and Penhallow (: 04), it is readily seen that the numerical distribution of these leaf forms in geological time cannot be regarded as affording an accurate basis upon which to found a knowledge of succession, and such remains can never be of more than approximate value with reference to an exhibition of the most general relations. Under these circumstances, as pointed out by Holm ('95) some years since, "a careful study of the recent flora is absolutely necessary when it is desired to identify fossil leaves with even an approximate degree of correctness. The plant must be studied as it stands amidst the surroundings to which it has adapted itself and which its leaves reflect." It is altogether probable that a more complete and detailed knowledge of the Salicaceæ would show that the present forms which are recognized as distinct species, in reality represent, in many cases, only variations of the same species.

This idea is emphasized more particularly in the case of the willows by the observation that *Salix protæfolia* has no less than four variants, or five forms in all, as presented by the generally accepted specific type and the varieties designated as *flexuosa*, *lanceolata*, *linearifolia*, and *longifolia* — forms which are all characteristic of the Dakota group, though *S. protæfolia* and *S. protæfolia flexuosa* are also found in the lower Cretaceous. We therefore find that so far as the geological evidence alone is concerned, it throws no light whatever upon the possible ancestry of these plants, it affords absolutely no clue as to their relations to other groups of plants, and it gives no very trustworthy information as to their present position in the scale of development. But when such evidence is taken in conjunction with that derived from a knowledge of the family as at present existing, the following conclusions appear to be fully justified :

(1) The Salicaceæ as a whole is an Old World family with its probable center of distribution in southeastern Europe and Central Asia.

(2) It is a family with a strong tendency to a boreal habit which has become more definitely emphasized since Tertiary time.

(3) The present tropical and subtropical members of the family, probably represent the relics of a wider dispersion in Cretaceous and Tertiary time, which have been isolated and localized as the result of more recent contraction in the family as a whole.

(4) The family at present affords strong proof of a temperate climate. In Cretaceous time it was compatible with a much warmer climate than at present, as indicated by the survival of tropical and subtropical forms ; but changes more recently effected, have made its tendencies boreal rather than tropical.

(5) The family had but a feeble development in the Lower Cretaceous, but become greatly augmented in the Middle Cretaceous.

(6) It is a family which may be regarded as still in process of development.

(7) The process of evolution is chiefly expressed in the genus Salix which shows a very great increase since the Middle Cretaceous.

(8) The process of evolution is less definitely expressed in the genus Populus which shows but little advance since the Middle Cretaceous, and it may possibly be regarded as having attained the culmination of its development.

While it is impossible at present to discuss the anatomy of these plants in the light of their ancestral forms, the study of existing species may serve an important purpose as a working basis for future paleontological research in this direction, and it may eventually prove to be the key which shall unlock the door now concealing important records of the past. In this sense it is necessary to formulate a theory of possible descent as a working hypothesis, and this can be obtained only through a detailed study of the anatomy of the Salicaceæ in comparison with what has already been ascertained to represent certain laws of development in the gymnosperms. This hypothesis may be stated briefly before proceeding to a discussion of those anatomical details which may lend it support.

A comparison of the ferns, arborescent pteridophytes such as Calamites and Lepidodendron, and the arborescent types of gymnosperms and angiosperms, shows, in general terms, that the so called wood increases in proportion to the requirements of mechanical support. This latter is usually met by the disposition of the tissue in such a manner as to afford the most effective resistance to external stress, and it is therefore disposed in monostelic stems, in the form of a definite cylinder which constitutes the secondary xylem structure. It is also an essential feature of the same law, that the secondary xylem should be in all cases radially external to the protoxylem, and that its augmentation in secondary growth of the stem must always arise in radial succession.

In the polystelic ferns where the secondary xylem consists almost wholly of vessels and the wood elements are numerically subordinate, these latter are distributed among the other elements of the xylem and do not form a specialized mechanical region. Such strengthening as these plants require, is accomplished in the first instance by the sclerenchymatous bundle sheath, and secondarily by the more general conversion of the fundamental tissue into hard sclerenchyma. It is similarly

impossible to compare such plants in any direct way with the polystelic angiosperms in which the mechanical tissue generally encloses the vascular structure in a more or less definite sheath which exhibits a more or less clearly defined relation to mechanical stress. While, therefore, for the purposes of our present argument, it is impossible to introduce exact comparisons with any of the polystelic forms of stems, we must nevertheless conclude that the secondary wood, in whatever form it may be disposed, must be regarded as differentiated to meet mechanical ends as shown by Williamson ('71) in his various elaborations of the Calamitean structure and as more recently stated by White (:05); but a knowledge of the relations existing between the protoxylem and the secondary xylem requires a more critical examination in detail, in order to determine the course of development which has given to the gymnosperms and the dicotyledonous angiosperms, the peculiar structural aspects distinguishing them respectively. This will constitute the subject of a special paper at a future date, and in the meantime it will serve our present purpose to state briefly the fundamental conceptions which form the essential features of our hypothesis. In order to make our point of view more clear, it will first be necessary to state concisely what has been shown to hold true of the gymnosperms with respect to the evolution of the secondary vascular structure and its economic aspects in relation to the requirements of support, as well as its physiological *rôle* in the conveyance of nutrient fluids.

The origin of the gymnosperms in the Cycadofilices, or at least a portion of them, is now generally accepted as an established fact. The essential starting point for the evolution of the vascular cylinder is therefore to be found in the scalariform and spiral vascular elements of the Cycadofilices or their filicinean ancestors which constitute the entire vascular bundle of those plants, and which, in the gymnosperms, constitute the protoxylem structure only. The relatively greater extent to which the mechanical elements are developed in some of the Cycadofilices and in the Cycadaceæ as a whole, is in direct response to the somewhat more arborescent tendency of these groups as particularly expressed in certain genera; while the fact that they do

not in any case attain to the extreme preponderance noted in the
Cordaitæ and Coniferæ, etc., is precisely in harmony with the
general approximation of the Cycadaceæ as a whole to their
filicinean ancestors and the lack of need for that peculiar form
of mechanical support which is demanded by trees of large size,
and which is provided in all the arborescent forms of the seed
plants. With these statements it will be unnecessary to follow
the Cycadaceæ in further detail, but rather to consider the
course of events in the more arborescent Cordaitales and Conif-
erales where the analogy with the angiosperms is closest. It is
now a well recognized fact that the protoxylem of the gymno-
sperms constitutes a transition zone within which peculiar and
often somewhat remarkable evolutionary changes take place.
The protoxylem or transition zone is a region peculiarly sensi-
tive to the controlling influences of environment, and its response
is so immediate as to give rise to structures of a very diverse
nature. This has been shown to be true of the Cycadaceæ
(Penhallow, : 04c) to a notable extent, while it is no less promi-
nent in the Cordaitæ, both of which groups are of a recognized
primitive character among gymnosperms and stand in somewhat
close relations to their Cycadofilicinean ancestors. But a very
important difference exists between these two groups with respect
to the survival of the protoxylem and the precise composition
of the secondary wood. In the Cycadaceæ the growth of the
stem in annual increments involves the complete repetition of the
entire xylem structure and the formation of secondary growth
in a manner which is to be met with in no other group of gym-
nosperms. The growths of successive years are not immedi-
ately joined to one another and therefore conterminous, but they
are separated radially by very definite zones of fundamental
tissue of the original cortex. In each zone of growth we recog-
nize spiral and scalariform elements of a transitional form,
together with tracheids bearing bordered pits and forming the
secondary xylem. These tissue regions are disposed precisely
as in the growth of the first year; they bear the same relations
to one another both in position and in development, and in each
case they perform the same functions as in the initial zone.
From this it follows that there is a complete regeneration of the

xylem structure in all its parts, with each year of growth, and it is not unreasonable to consider that the same structural regions should be designated by the same terms wherever they may occur. In this sense, therefore, we should recognize the primary growth, as well as the secondary growth of each subsequent year, as composed in each case of protoxylem and secondary xylem. The protoxylem survives throughout the entire life of the plant.

In the higher gymnosperms as also in the Dicotyledonous angiosperms, the case is quite different. In them the rings of secondary growth are in all cases united to and conterminous with the structure of the preceding year, and under these circumstances, as well as for reasons which will again be referred to, the protoxylem experiences complete suppression and does not reappear after the growth of the first year. In this case, then, the primary growth consists of protoxylem and secondary xylem, while the secondary growth consists altogether of secondary xylem, and in this we find one of the most important structural distinctions between the Cycadaceæ and all other types of gymnosperms, bringing the former into the closest relations with their ancestral forms and removing the other gymnosperms with the Cordaitales as the basal member of the series, to a distinctly higher phylogenetic position.

In Cordaites, reduction has been developed to such an extent that the protoxylem no longer forms a constituent part of the annual rings of growth, since it is wholly confined to the growth ring of the first year where it constitutes a region of very considerable radial extent, gradually merging with the secondary xylem in such a way that there is no sharp line of demarcation between the two. Within this zone graduated transitions are a well known and remarkable feature; but it is to be noted that in all these respects there is a further removal from the ancestral forms and a distinct development along those lines of evolution which eventually issue in the characteristic structure of the higher Coniferales. As these latter are reached, it is to be observed that there is a constantly greater reduction in the radial extent of the transition zone, and the intermediate structural variations which it presents, until, eventually, it becomes

only a few elements broad, and there is an abrupt transition
from spiral or scalariform structures to the tracheids with bor-
dered pits.   We may therefore consider that in all the higher
Coniferales, the structural type is fixed to such an extent that
evolutionary aspects are no longer presented.

The changes initiated in the transition zone relate to the evo-
lution of the modified vessels or tracheids which constitute the
bulk of the structure in the vascular cylinder.   In the develop-
ment of such tracheids their capacity for the movement of the
transpiration current is not lost, except in special cases, but it is
rather modified with reference to the total extent of the conduc-
tive tissue and the somewhat low rate at which the transpiration
current is required to move.   Each tracheid is provided, among
the primitive forms, with bordered pits on both the radial and
tangential walls through which a somewhat ready and direct
transverse diffusion is provided for, while diffusion in a longi-
tudinal direction can never be otherwise than indirect and there-
fore at a relatively slow rate.   With an advance in organization,
the bordered pits tend to disappear from the tangential walls
where they survive only at the ends of tracheids or in the sum-
mer wood, the latter distribution being necessitated by the
peculiar radial compression which such cells experience.   It
follows from this that in all the higher types of the gymno-
sperms, there is a greater degree of restriction imposed upon
the transverse diffusion and through the latter, also a further
restriction of the longitudinal diffusion.   Whatever deficiency in
circulation is developed through these structural alterations,
compensation is provided by the great extent to which such tis-
sue is formed ; and that the tracheids effectively discharge the
duty imposed upon them in this respect is manifested in their
complete replacement of the true vessels of the protoxylem, as
well as in the fact that those of the heart wood may resume
their functional capacity for the conveyance of nutrient fluids
when the sap wood becomes incapacitated through desiccation
or other causes (Goodwin, '88).   Such restricted movement of
the transpiration current is in direct accord with the generally
xerophilous character of the gymnosperms, whether this latter
be correlated with absolute deficiency of water supplies or a

temperature which is so reduced as to permit of but slight ab-
sorbent activity in the roots ; and so it is found that the pecul-
iar form of the conductive tissue is really developed in correlation
with the environment of the plant.   But it is to be observed that
the protoxylem is called upon, in the course of its development,
to meet another essential factor in the life of the plant, namely,
its ability to withstand external stresses of various kinds and
through this the establishment of an upright position for the
organism.   It is quite conceivable that this requirement might
be met by the evolution of a specialized form of element from
the meristem without reference to the prior development of
vessels, and this might be looked for in the angiosperms, but
such has certainly not been the case in the gymnosperms.   The
somewhat slight modification, and in some senses the reduction
which the vessels of the protoxylem have undergone in their
adaptation to the movement of the transpiration current, has
also permitted of their immediate adaptation to the purposes of
mechanical support.   They have therefore become more fibrous
in character, while at the same time their walls have become
sensibly thickened and in corresponding degrees more fully
fitted to withstand stress.   It is thus evident that two forms or
directions of development have been combined in the same ele-
ment, and it is no doubt also true that the peculiar form of the
pits is in itself a direct resultant of such a combination develop-
ment, since it has been shown that the bordered pit represents
a localized area which has been left over in the otherwise gen-
eral thickening of the wall in response to the requirements of
intercellular circulation.   The reduction of the bordered pit and
its frequent elimination from the wall of the tracheid, especially
in the summer wood, is in direct harmony with these statements
and represents the relative predominance of requirements relat-
ing to circulation or mechanical support at different periods of
growth and under special conditions of environment.   So far as
we know at present, no further modification of the tracheid
than that presented in existing species is possible to the gymno-
sperms, and this particular line of evolution may therefore be
regarded as completed in that group.

Our hypothesis as applied to the angiosperms on analogous

lines of development, is based primarily upon the idea that the
well marked differentiation of conductive and mechanical tissue
which is everywhere so prominent a feature of the arborescent
forms, extending in a less conspicuous way to herbaceous types,
cannot be secondary to and therefore derived from that special
course of development which is so fully expressed in the wood
of the gymnosperms ; but that it must have had its origin in
antecedent or contemporaneous types, and that it must in conse-
quence represent a wholly distinct line of evolution arising in
response to very dissimilar environmental conditions.

In the angiosperms, representing as they unquestionably do, a
higher type of development, there is, even among their most
primitive forms, a further removal from the ancestral type, and
as presented by the Dicotyledons, they must be regarded as
essentially occupying the same general plane of development as
the higher Coniferales, inasmuch as they are all characterized
by a transition zone consisting of but few protoxylem elements ;
and the passage from these latter to the elements of the second-
ary xylem, whether vessels or wood cells, is abrupt and direct.
Like the higher Coniferæ, therefore, they represent types in
which the structure of the transition zone is essentially fixed,
and under normal conditions of development the formation of
the secondary xylem is, from the first, in direct response to a
fixed habit.   We may nevertheless expect that under exceptional
conditions of growth such as would involve reduced vigor, and
also such as through an induced habit of growth would eliminate
very largely the special necessity for mechanical support, there
would be a more or less marked tendency in the direction of
reversion to primitive structural conditions.   Such reversions
might be expected to show a distinct augmentation of the transi-
tion zone with the appearance of transitional forms of the ana-
tomical elements, which would then diverge from the protoxylem
in the particular directions imposed by the natural fixed habits
of the genus or species as the case might be.   Alpine forms
of otherwise large trees might be expected to afford the most
favorable material for the exhibition of such reversions in conse-
quence of (1) the greatly reduced form and size of the plant
consequent upon its unusual environment, and (2) the fact that

a dwarfed or even prostrate habit of growth no longer imposes those demands for rigid support which are from the first a prime necessity of the strictly arborescent forms.   Precisely such conditions and precisely such results are to be met with in *Salix cutleri* Tuckerm., of which a more detailed account will appear on a subsequent page.

In the development of the secondary xylem of angiosperms, two distinct lines of evolution are to be observed — the one leading to the exaggerated development of vessels, the other leading to the exaggerated development of mechanical tissue, the two being balanced with respect to the relative excess of requirements on the one side or the other.   Confining our attention in the first instance to the vessels, it is found that in their evolution from the elements of the protoxylem, these latter deviate more widely from a fibrous form so that their products become broader and either actually or relatively shorter, while the terminal walls often disappear altogether, thus giving rise to tubular structures of indeterminate length.   The walls of such vessels are somewhat modified by secondary thickening, though relatively to their usually great breadth this is not more than is demanded by their own need for support, and it cannot be regarded as an essential factor in the strength of the organism as a whole.   Like the tracheids of the Coniferae, the walls are characterized by the presence of bordered pits which differ in two very important respects from the similar markings which generally characterize the higher gymnosperms.   They are always multiseriate and chiefly hexagonal, though as shown in the Salicaceæ, they may become more distant and definitely rounded ; they also occur on both the radial and tangential walls.   In both of these features the vessels show the survival of primitive characteristics which are only partially represented among the Cordaitales, and which indicate that the ancestral forms must be looked for among the Cycadofilices where they are of well known occurrence, or else among some other group of similar structural characteristics, but of which we have no present knowledge.   Now the angiosperms are essentially all broad-leaved plants adapted to a distinctly mesophytic habit, and it is therefore to be concluded that the transpiration current not only moves with greater rapidity

as compared with the Coniferæ, but that it is of greater volume
and requires a correspondingly more capacious channel; while
such channels must also be direct and involve fewer impediments
to free circulation in a longitudinal direction.   These require-
ments are met by the large, transverse volume of the individual
vessel; by the great multiplication of vessels so characteristic of
Catalpa, Salix, Populus, etc.; by their repetition in the secondary
xylem of each year's growth, and in the provision for very free
longitudinal movement of fluids as expressed in the sieve-like
terminal walls, or in the complete obliteration of such interposed
septa.   Although such vessels retain their capacity for the con-
veyance of the nutrient fluids for a long time, *i. e.*, several years,
they eventually become functionless, often through the forma-
tion of extensive thyloses as in the Catalpas, members of the
Salicaceæ, Quercus, etc., and in general terms the functional
capacity of the vessels cannot be restored when so lost, while
under certain circumstances, the development of thyloses may
assume a definitely pathological aspect (Watt, :01).   From the
observations thus far made, it is evident that the particular evo-
lution of the protoxylem which results in the formation of such
vessels, provides elements which are solely concerned in the
movement of the transpiration current, and which have, as it
were, appropriated this function in such an exclusive sense as to
eliminate it from all other structural elements of the xylem, so
that these latter are thereby left free to develop in the most
responsive way under the special influence of other requirements.

We may now ascertain the special features which serve to dis-
tinguish the second course of evolution from the protoxylem,
already referred to.   The excessive development of the conduc-
tive tissue tends to diminish the general strength and call for
the formation of purely mechanical elements to an extent other-
wise unnecessary.   This factor operates, therefore, to emphasize
the divergence of the two lines of structural evolution, giving
greater prominence to the conductive elements on the one hand
as already shown, and on the other hand to the mechanical ele-
ments.   Certain of the protoxylem elements, otherwise potential
vessels, are diverted in growth, and instead of expanding, they
contract with a correspondingly greater development of the sec-
ondary wall, and assume a strictly fibrous form.   This necessa-

rily leads to the greater simplification of the pits which rarely retain the bordered form but become simple perforations and commonly disappear altogether. Concurrently with these changes, the progressive increase in the thickness of the wall eventually leads to a more or less complete obliteration of the original cell cavity ; and while all these varied changes have a profound bearing upon the ultimate strength of the general structure, they at the same time operate to eliminate completely even such slight capacity for conduction of fluids as the elements may have had in their earlier stages of development.

The hypothesis as thus presented, is suggested at the present time in view of the many facts which have come under observation during the progress of studies bearing more particularly upon the anatomy of the Coniferales as elsewhere recorded (Penhallow, : 04c), and because of the need of some working basis from which we may view the anatomy of the Salicaceæ, and upon which we may erect a possible point of departure for an interpretation of their phylogeny. The first real test of the validity of this hypothesis will be made on the basis of data to be derived from a study of the Salicaceæ as recorded in subsequent pages. If it proves to have the support of observed facts it will then be necessary to supplement it with the further hypothesis that the angiosperms as a whole had their origin in some generalized type, possibly identical with or at least nearly related to the Cycadofilices ; and in any event we can hardly agree with the suggestion of De Vries (: 05) that the Monocotyledons "are obviously a reduced branch of the primitive Dicotyledons," since our own investigations not only fail to lend support to such an idea, but they tend to establish evidence to the contrary, and to the effect that while the two may possibly have had their starting point in a common, generalized type, they nevertheless represent two distinct lines of descent. On the basis of such a hypothesis, we should reasonably expect to find in the early Mesozoic and Permian, and possibly even in the later Carboniferous, transitional forms which would carry the angiosperms back to some of the later but less highly specialized types of the Cycadofilices.